A REVIEW OF THE SHORE-FLY GENUS *DIPHUIA* CRESSON (DIPTERA: EPHYDRIDAE)

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Abstract.—Diphuia Cresson is reviewed to include (1) the synonymy of *D. nasalis* Wirth with *D. nitida* Sturtevant and Wheeler, (2) the description of **D. flinti, new species** (Dominican Republic: El Seibo), and (3) a cladistic analysis of the genus.

Key Words: Diptera, Ephydridae, shore flies, Diphuia, New World tropics, cladistics

While conducting field work on the Dominican Republic in 1995, a tiny, somewhat shiny, black shore fly of the genus *Diphuia* Cresson was discovered that is apparently associated with freshwater habitats. Other species of *Diphuia* occur along shorelines and beaches of maritime environments with brackish-water or saline habitats. Determining the identity of this species, which is less than 2.5 mm in length, has led to this review and cladistic analysis of *Diphuia*.

Dipluia is known only from the New World, mainly from subtropical and tropical zones, and has greatest diversity in the Caribbean and adjacent areas. Although comparatively common in nature, specimens are scarce in collections, probably because of the restricted distribution of the genus and the small size of specimens (2.5 mm or less). The nomenclatural history of Diphuia and included species, as well as other available information were included in my earlier revision (Mathis 1990) and are not repeated here except for the taxa being treated.

METHODS

The terminology and methods used in this study were explained previously (Mathis 1990). Because of the small size of specimens, study and illustration of the male terminalia required the use of a compound microscope. To better assure effective communication about structures of the male terminalia, I have adopted the terminology of other workers in Ephydridae (see references in Mathis 1986). Usage of these terms, however, should not be taken as an endorsement of them from a theoretical or morphological view over alternatives that have been proposed (Griffiths 1972, McAlpine 1981). Rather, I am deferring to tradition until the morphological issues are better resolved.

Two venational ratios are used commonly in the descriptions and are defined here for the convenience of the user (ratios are averages of three specimens).

- 1. Costal vein ratio: the straight line distance between the apices of veins R_{2+3} and R_{4+5} /distance between the apices of veins R_1 and R_{2+3} .
- 2. M vein ratio: the straight line distance along M between crossveins (dm-cu and r-m)/distance apicad of crossvein dm-cu.

The specimens used in this study are primarily in the National Museum of Natural History (USNM), Smithsonian Institution. A few, especially primary types, are in the American Museum of Natural History

(AMNH), New York. I also examined specimens from the University of Texas, Austin (UTA) collection.

The phylogenetic analysis was performed with the assistance of Hennig86 ©, a computerized algorithm that produces cladograms on the basis of parsimony. Before performing the analysis, the character data were arranged in transformation series and then polarized primarily using outgroup procedures.

Diphuia Cresson

Diphuia Cresson, 1944:4. Type species: Diphuia anomala Cresson, 1944, by original designation; 1946:138, 140 [note, key].—Sturtevant and Wheeler, 1954:248 [notes].—Wirth, 1956:4 [discussion of species]; 1965:737 [Nearctic catalog]; 1968:5 [Neotropical catalog].—Mathis, 1990:746–756 [revision].—Mathis and Zatwarnicki, 1995:155–156 [world catalog].

Description.—Mostly black, subshiny to shiny, microtomentum usually sparse; small shore flies, length 1.35-2.10 mm. Head: Wider than high; face width-to-head width ratio 0.28; frons black, mostly unicolorous, lacking distinctively colored ocellar triangle; frons wider than long, frontal lengthto-width ratio 0.58; frontal vestiture variable; ocellar seta well developed, inserted slightly in front of alignment of anterior ocellus and at about the same distance apart as between posterior ocelli; pseudopostocellar setae usually well developed, length subequal to ocellar setae, proclinate, slightly divergent; 1 reclinate and 1 proclinate fronto-orbital seta present, reclinate seta inserted slightly anteromediad of proclinate seta; both inner and outer vertical setae present; ocelli arranged to form isosceles triangle, with distance between posterior ocelli larger than between anterior ocellus and either posterior ocellus. Antenna exerted; pedicel with well-developed, proclinate, dorsal seta; aristal length subequal to antennal length and bearing 4–5 dorsal rays, with

basal 3 rays longer than apical 1-2, the latter subequal. Eye apparently bare of microsetulae (using a stereomicroscope). Face black in both sexes and with silvery white, microtomentose antennal grooves and with 2 lines, sometimes irregular, paralleling parafacials, these and similarly invested and colored ventral margin (microtomentum sometimes interrupted at middle) form a facial triangle that has a small microtomentose area below facial prominence; face not carinate between antennal bases but slightly, conically protrudent at middle (best seen in lateral view); ventral facial margin shallowly emarginate; face bearing 2 facial setae, the dorsal seta very slightly larger, both inserted near parafacials; parafacials densely microtomentose, silvery white; clypeus very sparsely microtomentose, black; palpus blackish brown to black; mouthparts not geniculate, labella shorter than mediproboscis. Thorax: Generally black, vestiture of microtomentum variable with species, although generally sparse; pleural areas lacking stripes of distinctly colored microtomentum. Chaetotaxy with mesonotal setae poorly developed except for those at posterior margin; mesonotal setulae numerous and not arranged in well-defined setal tracks; prescutellar acrostichal setae much larger than other acrostichal setulae and more widely set apart; only 1 dorsocentral seta, inserted posteriad; intra-alar setulae irregularly seriated; presutural seta well developed, length subequal to notopleural setae; 2 scutellar setae and scutellar disc with sparse, scattered setulae; postpronotal seta 1; postalar seta 1; notopleural setae 2, insertion of posterior seta elevated dorsally above anterior one; anepisternal setae 2, inserted along posterior margin; katepisternal seta well developed, conspicuous. Wing: membrane mostly hyaline to very slightly milky white; veins behind costa pale, usually yellowish to yellowish brown; vein R₂₊₃ extended well beyond level of crossvein dm-cu, 2nd costal section at least 11/2 times longer than 3rd section; alular marginal setulae short, less than ½ alular height.

Legs: femora black; tibiae dark basally, concolorous with femora, apices yellowish. *Abdomen:* Fifth segment of male well sclerotized, elongate, not normally visible from a dorsal view, usually retracted within 4th segment; 5th tergum and sternum of male united anteriorly to form a complete annulus. Male terminalia as follows: cercus rod shaped, bearing 1–3 conspicuously longer setae at ventral margin; surstylus well developed, well sclerotized, conspicuous, and as long or longer than cercus.

Distribution.—New World. Temperate to tropical zones, in North America along the east coast (New York south to Florida) and the Caribbean to Colombia and Ecuador in South America.

Diagnosis.—Diphuia can be distinguished from other genera of Hecamedini as follows (characters indicated by an asterisk (*) are autapomorphies that corroborate the monophyly of Diphuia): *coloration very dark, usually black; *microtomentum of head and thorax generally sparse, giving a subshiny to faintly dull appearance; facial coloration of male and females similar, lacking sexual dimorphism; face, although slightly protrudent medially (best seen in profile), not acutely pointed in lateral view; *face with silvery white microtomentose markings, antennal grooves, 2 vertical lines, ventral margin, an area below the facial prominence, and parafacials; presutural and prescutellar setae well developed; *pleural region lacking a stripe or stripes; 5th segment of male well sclerotized and its tergum moderately elongate; *5th tergum and sternum of male united anteriorly to form a complete annulus; and male genitalia with distinct, well-sclerotized, elongate surstyli.

KEY TO SPECIES GROUPS AND SPECIES OF *DIPHUIA*

 Anepisternum with anteroventral ½-½ bare, shiny black, otherwise with sparse investment of whitish gray microtomentum; mesonotum sparsely invested with microtomentum, subshiny; 5th tergum of male with anterior margin

even (Fig. 2); surstylus with ventral margin broadly rounded; gonite trapezoidal; aedeagus with apex bifurcate D. nitida Sturtevant and Wheeler Anepisternum almost entirely invested with whitish gray microtomentum; mesonotum moderately densely microtomentose, golden brown; 5th tergum of male shallowly or deeply emarginate (Fig. 16); surstylus truncate ventrally, pointed apically; gonite with basal half subrectangular; aedeagus not bifurcate apically 2. Ventral portion of face with median, vertical, densely microtomentose, silvery white stripe extended dorsad from and connected to microtomentose ventral margin; 5th tergum longer than wide, anterior margin shallowly emargin-Ventral portion of face with median, densely microtomentose, silvery to golden white spot (frequently triangular or diamond shaped) that is not directly connected with microtomentum along ventral margin; 5th tergum wider than long, anterior margin deeply emarginate, emar-3. Surstyli long and narrow, length subequal to that of cercus; gonite pointed posteroventrally; aedeagus only moderately curved apically D. anomala Cresson Surstyli moderately short and robust, length shorter than cercus; gonite with posteroventral portion broadly bifurcate; aedeagus more

Diphuia nitida Sturtevant and Wheeler (Figs. 1–8)

curved apically, point oriented anteriorly ...

Diphuia nitida Sturtevant and Wheeler, 1954:248.—Wirth, 1965:737 [Nearctic catalog].—Mathis, 1990:754 [revision].—Mathis and Zatwarnicki, 1995: 156 [world catalog].

Diphuia nasalis Wirth, 1956:3; 1968:5 [Neotropical catalog].—Mathis, 1990: 750–754 [revision].—Mathis and Zatwarnicki, 1995:156 [world catalog]. New Synonym.

Description.-Small shore flies, length 1.35 to 1.75 mm.

Head: Frons sparsely invested with fine brownish microtomentum, microtomentum becoming sparser or lacking on 2 small areas laterad of posterior ocelli, 2 spots along the anterior margin, and sometimes a small spot in front of the anterior ocellus. Ventral portion of face with median, densely microtomentose, silvery to golden white spot (frequently triangular or diamond shaped) that is not directly connected with microtomentum along ventral margin.

Thorax: Mesonotum sparsely invested with fine brownish to golden brown microtomentum, mostly subshiny to shiny; anepisternum with anteroventral ½ to ½ bare of microtomentum, shiny, posterodorsal portion invested with fine, grayish microtomentum. Wing with costal vein ratio 0.58; M vein ratio 0.40.

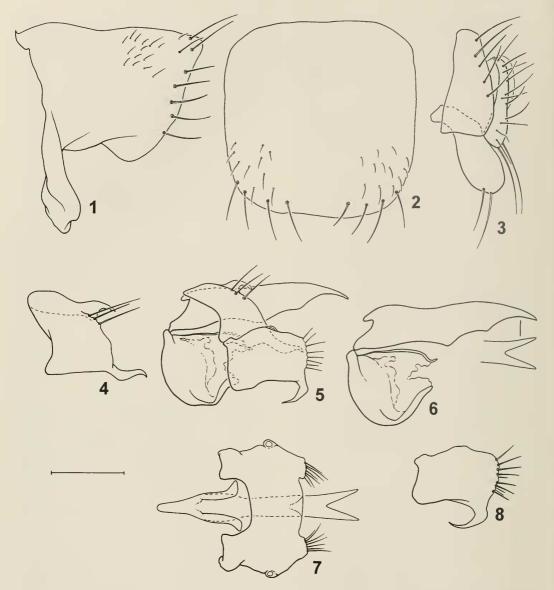
Abdomen: 5th tergum with anterior margin essentially straight, at most very shallowly arched anteriorly (Fig. 2); 5th sternum undivided, as a narrow band connected dorsally with anteroventral portion of 5th tergum (Fig. 1). Male terminalia (Figs. 3-8) as follows: epandrium narrow in lateral view, much higher than wide (Fig. 3); surstylus as long as cercus but almost twice its width, broadly rounded apically (Fig. 3); gonite in lateral view parallelogram-shaped, posterior angles produced into pointed processes, posteroventral process sinuous (Figs. 4-5); aedeagal apodeme rounded anteroventrally (Figs. 4–5); aedeagus acutely pointed apically, in dorsal or ventral view bifurcate apically (Figs. 4–5); hypandrium in ventral view wider than long, anterior margin shallowly arched anteriorly (Figs. 5, 7-8).

Type material.—The holotype ♀ of *D. nitida* is labeled "Dougl[a]s[t]on[,] L[ong]. I[sland]., N[ew]. Y[ork].[,] Au[gust]. 17, [19]52/HOLOTYPE Diphuia nitida Stvt & Whlr [pink]/TYPE 6695 [dark pink; number handwritten]." The holotype is point mounted, is in poor condition (the antennae and several setae are missing and the left side of the body and wings are covered partially with glue), and is deposited in the ANSP (6695). Sturtevant and Wheeler stated that this specimen is a male, but it is clearly a female.

The holotype \mathcal{P} of *D. nasalis* is labeled "Long Island[,] Deadman's Cay[,] March

11, 1953/Van Voast-A.M.N.H. Bahama Isls. Exped Coll. E.B.Hayden/&/&HOLOTYPE Diphuia nasalis W.W.Wirth [red, gender and species name handwritten]." The holotype is point mounted, is in good condition (tip of right wing folded back on itself), and is deposited in the AMNH. Although the holotype was listed as a male (Wirth 1956:4) and the specimen is so marked, it is a female.

Other specimens examined.—BAHA-MAS. Crooked Island, Landrail Point, 5 Mar 1953, E. B. Hayden, L. Giovannoli (1 9; AMNH); Exuma Cays, Staniard Bay, 13 Jan 1953, E. B. Hayden (1 ♀; AMNH); Long Island, Deadman's Cay, 11 Mar 1953, E. B. Hayden (2 ♂; AMNH, USNM). BE-LIZE. Stann Creek District: Bread and Butter Cay, 25 Mar 1988, W. N. Mathis (5 ♂, 1 ♀; USNM); Glover's Reef (Long Cay, Middle Cay, Northeast Cay, Southwest Cay), 26–28 Jul 1989, W.N. Mathis (29 ♂, 12 ♀; USNM); Man of War Cay, 8–15 Nov 1987, W. N. & D. Mathis (7 ♂, 4 ♀; USNM); Twin Cays (West Bay), 22 Mar 1988, W. N. Mathis (1 ♂, 1 ♀; USNM); Wee Wee Cay, 24-25 Mar 1988, 21 Jul 1989, W. N. Mathis (5 ♂; USNM). Six Belize, 1959, N. L. H. Krauss (1 &; USNM). BERMUDA. Hamilton Parish. Shelly Bay, 20 Nov 1987, D. J. Hilburn, N. E. Woodley (2 ♀; USNM). DOMINICAN REPUBLIC. Barahona: Cabral (canals E of Cabral; 18°15.2′N, 71°13.4′W), 16 May 1995, W. N. Mathis (1 ♂, 1 ♀; USNM). *La Romana:* Isla Saona, Catuano (18°11.7'N, 68°46.8'W), 13 May 1995, W. N. Mathis (1 ♂; USNM). GRAND CAYMAN. Governor Gore Bird Sanctuary (19°16.7'N, 81°18.5'W), 25 Apr 1994, W. N. Mathis (1 &; USNM). JA-MAICA. Falmouth (bay shore), 1 Mar 1969, W. W. Wirth (1 ♂; USNM); Milk River Bath (mangroves), 11 Mar 1970, T. Farr, W. W. Wirth (5 ♂, 1 ♀; USNM); Negril Beach (rocky shore), 12 Mar 1970, W. W. Wirth (1 ♂; USNM); Runaway Bay (bay shore), 16-28 Feb 1969, W. W. Wirth (3 ♂; USNM). UNITED STATES. Florida. Monroe Co., Bahia Honda Key (seashore), 11



Figs. 1–8. *Diphuia nitida*. 1, 5th tergum and sternum, lateral view. 2, 5th tergum, dorsal view. 3, Male terminalia (epandrium, cercus, surstyli), lateral view. 4, Gonite, lateral view. 5, Internal male terminalia (gonite, hypandrium, aedeagal apodeme, aedeagus), lateral view. 6, Aedeagus and aedeagal apodeme, lateral view. 7, Hypandrium, aedeagal apodeme, and aedeagus, ventral view. 8, Hypandrium, lateral view. Scale = 0.1 mm.

Apr 1970, W. W. Wirth (4 δ , 3 \circ ; USNM); Big Pine Key, 11-Apr-30 Dec, 1954, 1970, H. V. Weems (1 δ , 1 \circ ; USNM); Long Key, 23 Jun 1953, M. R. Wheeler (1 δ ; UTA); Saddlebunch Keys, 29 Dec 1953, H. V. Weems (1 δ , 1 \circ ; USNM). North Carolina. Onalow Co., Ashe Island, 11 Aug 1975, J. C. Dukes (1 \circ ; USNM).

Distribution.—Nearctic: USA (FL, NC, NY). Neotropical: Bahamas, Belize, Bermuda, West Indies (Dominican Republic, Grand Cayman, Jamaica).

Natural history.—The vast majority of specimens from the Belizean cays were collected by sweeping just above mangrove peat that is well shaded most of the day. A

few specimens, apparently feeding, were collected on flowers. The association with mangrove peat must be opportunistic, as the species occurs in areas where mangrove does not now exist.

Diagnosis.—This species is distinguished from congeners, especially *D. anomala* and *D. zatwarnickii*, by the sparsely microtomentose mesofrons; the subshiny mesonotum that is very sparsely invested with fine, golden brown microtomentum; the sparsely, whitish gray microtomentose anepisternum; the shiny anterior half of the katepisternum; and several characters of the male terminalia (see description and figures).

Remarks.—Since 1989, when the research from my earlier revision (Mathis 1990) was completed, I have studied longer series of specimens from additional localities. These studies indicate that D. nasalis and D. nitida are conspecific, with the latter being the senior synonym. Although no more specimens from the type locality (New York: Long Island, Douglaston) of D. nitida have become available. I now strongly suspect that the difference noted earlier between the nominate species has mostly to do with the poor condition of the holotype female of D. nitida. This specimen, which is the entirety of the type series, appears to have been "rubbed" (antennae and several setae are missing), which could also account for the shinier frons, the only distinguishing character.

Diphuia flinti Mathis, new species (Figs. 9–16)

Description.—Small to moderately small shore flies, length 1.60 to 2.10 mm.

Head: Frons sparsely and uniformly invested with fine brownish to grayish microtomentum. Ventral portion of face with median, vertical, densely microtomentose, silvery white stripe extended dorsad from and connected to microtomentose ventral margin.

Thorax: Mesonotum, including postpronotum and notopleuron, sparsely invested

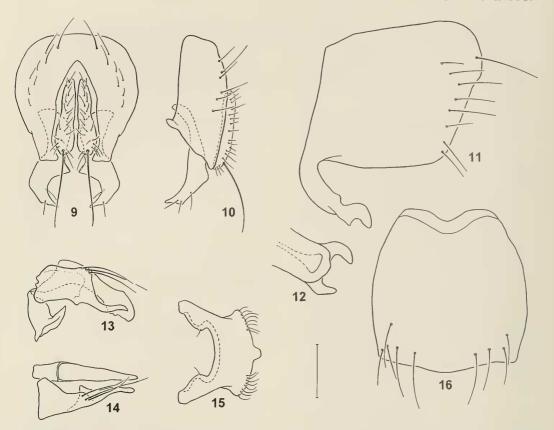
with fine brownish to golden brown microtomentum, mostly subshiny; anepisternum, anepimeron, and posterior half of katepisternum sparsely invested with fine, whitish gray microtomentum; anterior half of katepisternum with oval spot bare of microtomentum, shiny. Wing with costal vein ratio 0.58; M vein ratio 0.40.

Abdomen: 5th tergum with anterior margin emarginate medially (Fig. 16); 5th sternum a narrow arch that is connected anteriorly with 5th tergum (Fig. 11), apex with 2 flanges (Fig. 12). Male terminalia (Figs. 9-10, 13-15) as follows: epandrium higher than wide in lateral view, ventral margin pointed (Fig. 10); surstylus longer than cercus, obtusely angulate in lateral view, apex truncate and pointed medially and anteriorly (Figs. 9-10); gonite in lateral view with basal half subrectangular, with narrow, sinuous, pointed process apically (Figs. 13-14); aedeagal apodeme in lateral view irregularly triangular (Fig. 13); aedeagus rounded apically in lateral view (Fig. 13), pointed (not bifurcate) in dorsal view (Fig. 14); hypandrium in ventral view wider than long, anterior margin deeply arched with medial margins recurved, posterior margin evenly arched except for a short, median process (Fig. 15).

Type material.—The holotype δ is labeled "DOMINICAN REPUB. El Seibo: near Rincón[,] 18°45.3′N, 68°55.7′W[,] 12 May 1995, WNMathis/USNM ENT 00136995 [bar code label]." The allotype φ and 14 paratypes (10 δ , 4 φ) bear the same locality label as the holotype. Other paratypes are as follows: *DOMINICAN RE-PUBLIC. El Seibo*: El Seibo (5 km E; 18°44.73′N, 68°59.2′W; 120 m), 12 May 1995, W.N. Mathis (1 δ , 5 φ ; USNM). The holotype is double mounted (minuten in silicon plastic block), is in excellent condition, and is deposited in the USNM.

Distribution.—Neotropical. Dominican Republic (El Seibo).

Diagnosis.—I can distinguish this species only on the basis of structures of the male terminalia, especially the shape of the 5th



Figs. 9–16. *Diphuia flinti*. 9, Epandrium, cerci, and surstyli, posterior view. 10, Same, lateral view. 11, 5th tergum and sternum, lateral view. 12, Apex of 5th sternum, ventral view. 13, Gonite, aedeagus, and aedeagal apodeme, lateral view. 14, Left gonite and aedeagus, dorsal view. 15, Hypandrium, ventral view. 16, 5th tergum, dorsal view. Scale = 0.1 mm.

tergum, surstylus, gonite, aedeagus, and hypandrium as described and illustrated.

Natural history.—The type series was collected along the banks of the Rio Quisibani, which is a freshwater stream.

Etymology.—It is a pleasure to name this species after Dr. Oliver S. Flint, Jr., who accompanied me on the field work that resulted in the collection of this species.

PHYLOGENETIC CONSIDERATIONS

Diphuia is in the tribe Hecamedini (Mathis 1991a, 1991b, 1993) and belongs to the clade including Hecamede Haliday and Allotrichoma Becker, sensu lato, including Pseudohecamede Hendel (Mathis 1991a). This relationship is evidenced by the retracted fifth tergum of the male, which

is moderately elongate, almost tubular. *Diphuia* may be the sister group to the rest of the *Allotrichoma* clade, following Cresson's (1944) original assessment, although the evidence supporting this relationship is not compelling, and *Diphuia* could be mostly closely related to *Hecamede* Haliday.

The monophyly of *Diphuia* within Hecamedini is well established (see generic diagnosis for a partial list of synapomorphies), and the remainder of this section will be devoted to the phylogenetic relationships among the species. First the character evidence is presented, followed by a brief discussion that is intended to complement the cladogram.

Character evidence.—The characters used in the cladistic analysis are listed be-

Table 1. Matrix of characters used in the cladistic analysis of *Diphuia*.

	Characters								
Taxa	1	2	3	4	5	6	7	8	9
Outgroug	0	0	0	0	0	0	0	0	0
D. anomala	1	-0	1	2	- 1	1	- 1	- 1	- 1
D. zatwarnickii	1	0	1	2	1	1	- 1	- 1	1
D. nitida	0	1	0	0	-0	0	-0	0	- 0
D. flinti	0	()	0	1	1	1	1	1	0

low and the distribution of their states is shown in the matrix (Table 1) and discussed here. For each character, the plesiomorphic condition is indicated by a 0, and the relative apomorphic condition(s) is indicated by a 1 or 2.

- 1. Vestiture of mesonotum: (0) sparsely microtomentose, subshiny; (1) moderately densely microtomentose.
- 2. Vestiture of anepisternum: (0) sparsely, uniformly microtomentose; (1) anteroventral ½ to ⅓ bare, shiny.
- 3. Length of 5th tergum of male: (0) longer than wide (Figs. 1–2, 11, 16); (1) wider than long (Figs. 1–2, 16–17 in Mathis 1990).
- 4. Shape of anterior margin of 5th tergum of male: (0) straight, even; (1) shallowly emarginate; (2) deeply emarginate, V-shaped (Figs. 2, 17 in Mathis 1990).
- 5. Shape of ventral margin of epandrium: (0) broadly formed, somewhat truncate; (1) tapered to point.
- 6. Shape of surstylus: (0) rounded; (1) truncate ventrally, pointed.
- 7. Shape of gonite: (0) trapezoidal with sides more or less equal (Fig. 4); (1) somewhat rectangular, longer than high (Fig. 13).
- 8. Shape of posterior margin of hypandrium: (0) smooth and even; (1) with a small, median projection.

9. Shape of aedeagus: (0) slender, 3–4× longer than high in lateral view; (1) more robust, length in lateral view about twice height (Figs. 7, 21 in Mathis 1990).

Discussion.—Analysis of the character evidence (Table 2), all morphological and primarily from the male terminalia, resulted in a single cladogram (Fig. 17). The single tree resulted from the implicit enumeration (ie*) option of Hennig86 and has a length of 10 steps and consistency and retention indices of 1.00 and 1.00, respectively. The analysis of characters is given in Table 2.

The cladogram (Fig. 17) for the four species consists of three bifurcations, with *D. nitida* at the base and the remaining species as the sister group. The monophyly of the latter assemblage is established by characters four (1) and five through eight. The next bifurcation has *D. flinti*, which is known thus far only from the Dominican Republic, branching off and as the sister group to *D. anomala* and *D. zatwarnickii*. The monophyly of the *D. anomala* and *D. zatwarnickii* group is indicated by four characters (1, 3, 4(2), 9).

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Funding for this research project, es-

Table 2. Analysis of characters used in the cladistic analysis.

					_				0
Character:	1	2	3	4	5	6	7	8	9
Steps:	1	1	2	1	1	1	1	1	1
Consistency Index:	100	100	100	100	100	100	100	100	100
Retention Index:	100	100	100	100	100	100	100	100	100

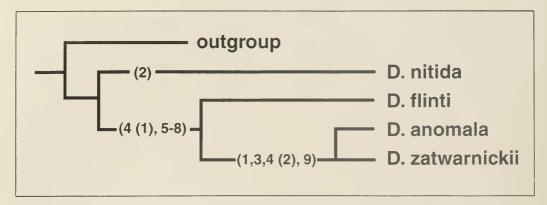


Fig. 17. Cladogram depicting hypothetical relationships among species of *Diphuia*. Tree length 10 steps, consistency index 1.00, retention index 1.00.

pecially the field work in Belize and the Dominican Republic, was provided by the Caribbean Coral Reef Ecosystems (CCRE) and Biodiversity Program (Biological Surveys and Inventories, BSI), National Museum of Natural History, Smithsonian Institution. This is contribution number 501 of the CCRE project, which is partially supported by a grant from the Exxon Corporation.

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